Thais emarginata (Deshayes): Description of the Veliger and Egg Capsule

BY

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(8 Text figures)

INTRODUCTION

Thais emarginata (Deshayes, 1839) is a small gastropod abundant on rocky shores from Alaska to Mexico (Ricketts & Calvin, 1962). It deposits eggs in a yellow, vase-shaped egg capsule. *Thais emarginata* undergoes non-pelagic development with the aid of nurse eggs.

The only species of *Thais* extensively studied to date is *Thais haemastoma floridana* Conrad, 1837 by D'Asaro (1966). D'Asaro describes the egg capsule and its formation, oviposition, and the embryology through the first planktotrophic veliger stage. He also gives an extensive summary of the work that has been done connected with the life histories of thaidids.

In the present paper, the egg capsules and non-pelagic veligers of *Thais emarginata* are described.

METHODS AND MATERIALS

A total of 98 egg capsules was collected from rocky areas north of Dillon Beach, California, on July 31 and August 10, 1970.

At the laboratory, the egg capsules were retained in 600 ml-capacity beakers in a refrigerator at 17° C. Embryos were removed from the capsule and placed in Stendor dishes for observation. Eggs and embryos were kept at the same controlled temperature. The filtered sea water was changed daily.

Terminology and criteria for measurements used in the description of the egg capsule are based on the generalized capsule shown in D'Asaro (1970). "Height is the distance from the apex to the basal membrane, width is the distance between the lateral edges at the widest point" (D'Asaro, *op. cit.*, p. 416).

Dimensions of shells are defined by the following criteria: width is the transverse distance of the aperture at the widest point; length is the distance from the shell rim to the far edge of the body whorl.

Measurements of the velum were taken at the widest point, from one lobe to the other.

All measurements were made from live animals with an ocular micrometer on a compound microscope. Illustrations were prepared from live animals, except for drawings of the shell which were made after the animal was removed.

OBSERVATIONS

Egg Capsule

The egg capsule of *Thais emarginata* is vase-shaped, pale yellow in color, with a short solid peduncle and a longitudinal suture that extends from the top of the peduncle to the rounded apex (Figure 1). The peduncle is flattened transversely to the suture and bordered by lateral ridges. A basal membrane of the capsule attaches to the substrate.

Capsules were found in crevices between *Mytilus* in mussel beds or directly attached to *Mytilus* shells. They were also found lower in the intertidal zone on exposed smooth rocks.

The capsule wall consists of 2 layers: an outer leathery layer which gives the capsule its characteristic shape, and an inner, loosely attached membrane that lines the interior and completely surrounds the embryos and nurse eggs. The inner membrane is transparent and cellophane-like in quality.

The escape aperture is capped with a hard, clear, gelatinous plug that extends above the escape aperture and is slanted toward and leads to the suture. The substance

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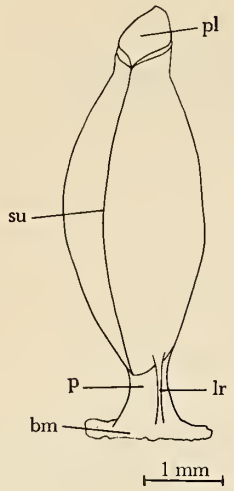

Figure 1

Egg capsule of *Thais emarginata*
bm – basal membrane lr – lateral ridge p – peduncle
pl – plug su – suture

of the plug appears to be identical with the inner lining of the capsule lumen.

The average dimensions of the capsule are: height, 5.9 mm; width, 2.3 mm; diameter, 2.2 mm. In comparison with those of *Thais haemastoma* and *T. rustica* Lamarck, 1819 (D'Asaro. 1966; 1970), the capsules of *T. emarginata* are rounded in cross section and show only a slight concavity on the side with the suture. Lateral ridges are found only on the peduncle.

The capsules are clustered together in irregular rows. The number of capsules per cluster ranges from 3 to 300 (Roy Houston, personal communication). One capsule can be attached to another so that clusters may be 2-layered. Sutures are aligned in the same direction.

Contents of the capsules vary from 64 to 750 eggs with an average of about 500 eggs. Most of these are unfertilized and serve as nurse eggs for developing embryos. Each egg is spherical and appears to be enclosed in a fine vitelline membrane. The average diameter is 180μ. Early cleavage was not observed.

The number of veligers found in the capsules ranges from 3 to 39, with an average of 16. The number of nurse eggs was found to be related to the developmental stage of the veligers. In the capsules of the earliest veligers there is an average of about 450 nurse eggs. In capsules containing the advanced veligers, there are no nurse eggs. A varying number of nurse eggs are present in capsules containing veligers between early and advanced stages. At early stages it was not possible to distinguish between eggs that would eventually develop and those that would remain as nurse eggs.

Shells

It was possible to some extent to determine the stage of veligers by examination of their shells. Observations were made on the shells of veligers in early, middle, and advanced stages of development. Average measurements were derived from 2 or more samples of empty shells, each collected from a healthy population of veligers.

The embryonic shell or protoconch is colorless and transparent. Directly after metamorphosis, brown and yellow pigmentations become prominent. Although the apparent shape varies greatly according to orientation, larval shells of *Thais emarginata* are simple and cup-shaped.

Only 2 early veliger shells were obtained. The first measured 335μ in length and 289μ in width. The second measured 277μ by 277μ. From a ventral view, the shells consisted almost entirely of aperture. The whorl was just beginning to develop. Both shells were very narrow in depth. The rim of the shells was smooth and faint striations were evident. In the first shell, 59μ of the lip consisted of a thinner, clear material without striations that appeared to be newly formed shell. This new formation was continuous around the shell, decreasing in width until it reached the whorl. It then extended 5μ from the edge of the whorl (Figure 2).

Sixteen mid-stage veliger shells have the following average dimensions: length, 550μ; width, 525μ. The

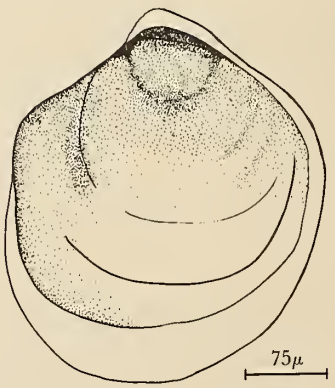

Figure 2

Early veliger shell of *Thais emarginata*

whorl has a $\frac{3}{4}$ turn. These have almost doubled in length and width. The appearance of the shell is similar to that of the early veliger shell, being clear, fragile, thin, and having some striations. This shell tends to collapse rather than break as do the more advanced shells. There is a heavy striation about midway down the shell. This marks the point where shell gland secretions end and mantle shell secretions begin. The average length of shell secreted by the shell gland is 325μ, which roughly corresponds to the total length of the early veliger shells (Figure 3).

Twenty-five advanced veliger shells have the following measurements: length, 775μ; width, 700μ. There is one complete whorl. The aperture takes up a little more than half of the total length of the shell. The rim has become more striated, but remains smooth. In all cases, the striations are faint (Figure 4).

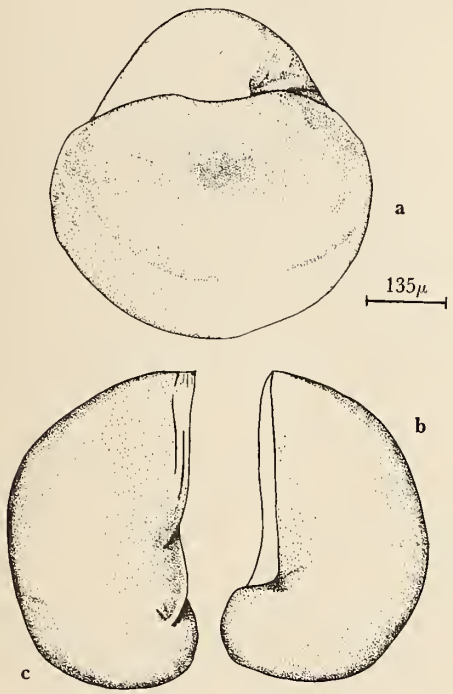

Figure 3

Mid-stage veliger shell of *Thais emarginata*
a: ventral **b:** right side **c:** left side

DESCRIPTION OF VELIGERS

Four veliger stages are described. Sequential time of development could not be monitored in this study because embryos removed from the egg capsule died within 2 days. Further, each cluster of egg capsules contained capsules with embryos in different stages of development so that following the development of veligers from clusters of capsules was not feasible.

Earliest Veliger

The body of the earliest veliger is round and measures 210 - 230μ in length. These veligers have considerable yolk and are often difficult to distinguish from broken nurse eggs, both of which are yellow in color.

Three ciliated areas are present on the embryo. The first ciliation occurs along a cephalic lobe. On one edge of the lobe is the second ciliated region, a protruding sensory area. These cilia are twice the length of cephalic lobe cilia. A third group of cilia occurs on a small protrusion, the shell gland, found laterally between the posterior of the animal and cephalic lobe (Figure 5).

Larval kidneys develop dorsolaterally to the cephalic lobe on each side of the embryo. These are produced by ectodermal proliferations (D'Asaro, 1966).

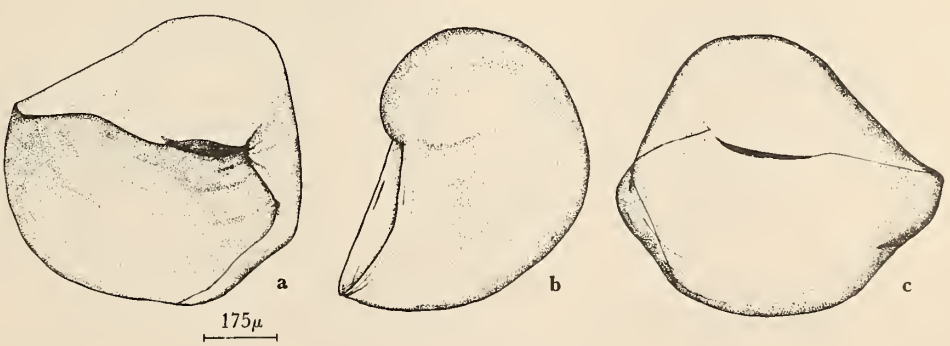

Figure 4

Advanced veliger shell of *Thais emarginata* **a:** ventral **b:** left side **c:** dorsal

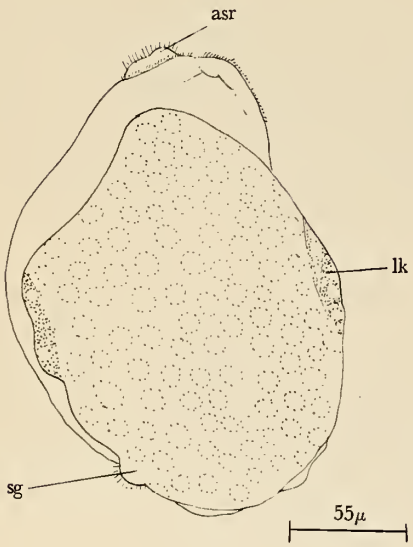

Figure 5

First stage veliger of *Thais emarginata*

asr – apical sensory region lk – larval kidney sg – shell gland

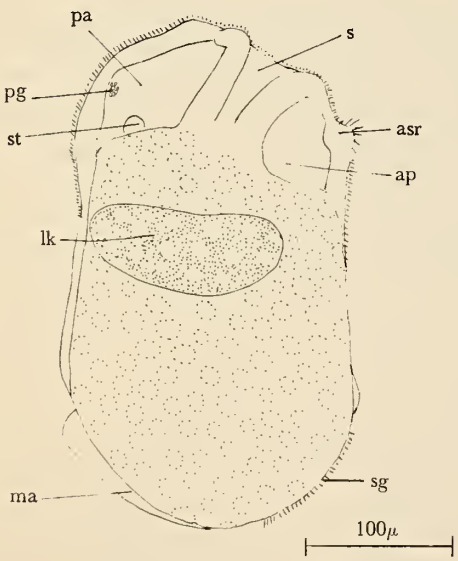

Figure 6

Second stage veliger of *Thais emarginata*

ap – apical plate asr – apical sensory region
lk – larval kidney ma – mantle anlage pa – pedal anlage
pg – pedal ganglia s – stomodaeum sg – shell gland
st – statocyst

Second Stage Veliger

This stage measures 240 - 370μ in length, is ovoid in shape, and still with a great deal of yolk. It is capable of rotation and forward and backward movement (Figure 6).

It is suspected that torsion occurs during the second veliger stage and is completed by the third stage. Evidence for this comes in the similarity of the second veliger stage to the torsional pause veliger described by D'Asaro (1966).

The cilia have developed further and cover considerably more area. The mantle anlage, stomodaea, pedal ganglia, and statocyst anlage have developed, while the larval kidneys have enlarged. The stomodaeal invagination is visible and seen to be deep enough to touch the anterior wall of the archenteron. Because of this invagination, the cephalic plate has been divided into 2 areas: an apical plate region that will eventually develop into the velar lobes, and a foot rudiment. Ventral to the stomodaeum on the foot rudiment is the pedal ganglion. Statocysts arise as invaginations dorsal to the pedal ganglia. Active oral ciliation is present in the stomodaeum and laterally on either side of the cephalic region and along the foot from the ventral lip of the stomodaeum to the anterior end of the pedal anlage.

The shell gland is heavily ciliated. This region outlines the anlage of the post-torsional dorsal mantle lip. The protoconch is formed from secretions of the shell gland.

Third Stage Veliger

The body of the third stage veliger is more elongated and measures 630 - 660μ in length. The shell encloses about one third of the body. The apical plate has differentiated into 2 small velar lobes. These measure 500μ from lobe to lobe and are bordered by cilia 40μ in length. This embryo uses the cilia of the velar lobes and is capable of gliding movements in any direction (Figure 7).

The entire oral region is ciliated. A short esophagus, usually filled with ingested nurse eggs, is visible. The esophagus probably leads into the gastric stomach, but because the body mass contains so much yolk, it is not possible to discern any additional internal structure.

A larval kidney, made up of vacuolated cells, lies directly behind each velar lobe. Towards the end of this stage, the larval kidneys decrease in size. The adult kidney, which is yellow in color and developing in the pleural groove, is presumably functional in the advanced veliger stage. The rhythmically beating heart is found just posterior and dorsal to the left larval kidney.

During this stage the mantle lip grows and becomes ciliated. Pedal ganglia are not evident. Statoliths are present in the statocysts dorsal to the mouth and between the larval kidneys.

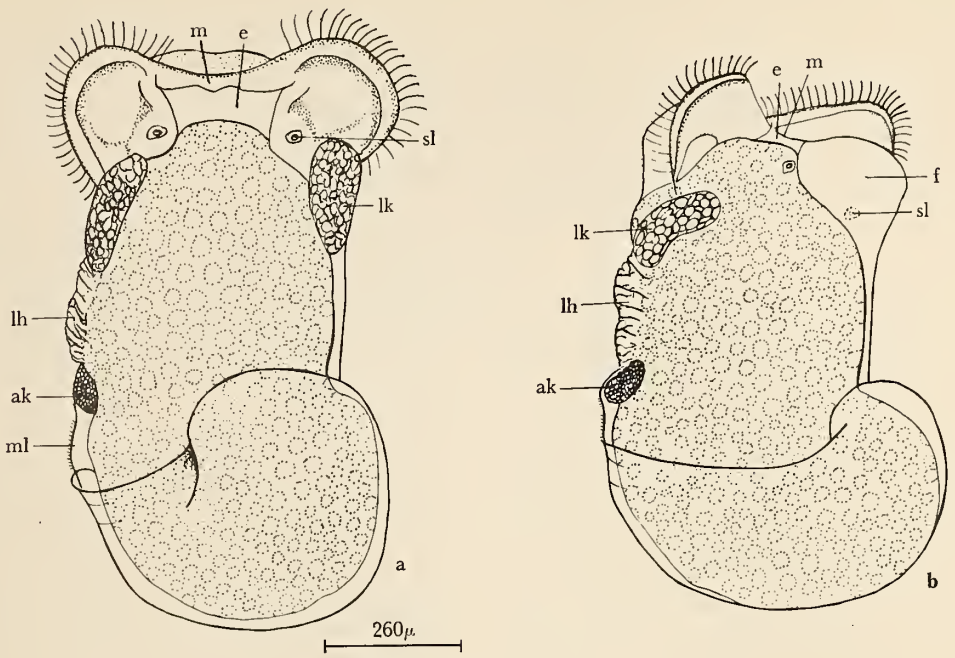

Figure 7

Third stage veliger of *Thais emarginata*

a: ventral b: left side lk – larval kidney m – mouth ml – mantle lip
ak – adult kidney e – esophagus f – foot lh – larval heart sl – statolith

The foot is clearly differentiated from the oral area, is small and ciliated. It is not used for locomotion. An operculum was not observed.

The columella muscle is located at the apex of the shell whorl. Muscle strands are difficult to trace due to the closeness of the mantle to the body mass.

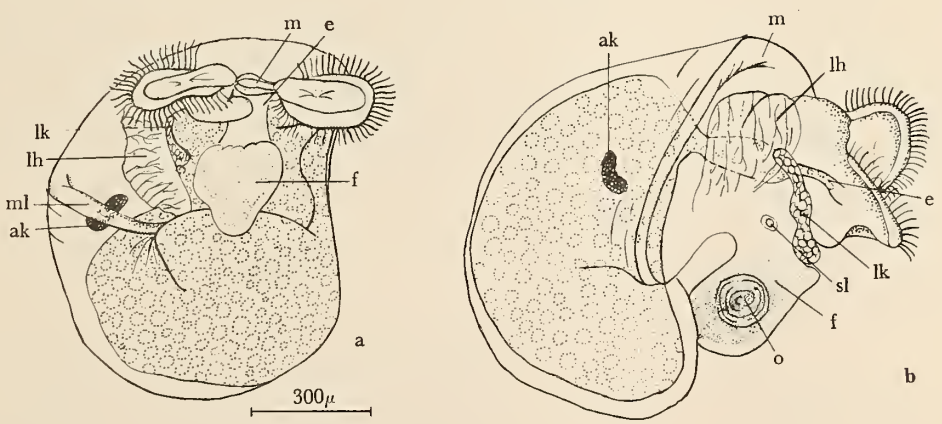

Figure 8

Fourth stage veliger of *Thais emarginata*

a: ventral b: left side lk – larval kidney m – mouth ml – mantle lip
ak – adult kidney e – esophagus f – foot lh – larval heart o – operculum sl – statolith

External changes in the cephalic region include formation of the right tentacle anlage, from which the right tentacle develops.

Several veligers were observed feeding on nurse eggs. A nurse egg was first rotated by the velar cilia until the egg became irregular in shape. The velar cilia seemed to weaken the membrane around the nurse egg, at which time oral cilia pulled the yolk through the mouth and into the esophagus.

Advanced Stage Veliger

The advanced veliger is almost entirely surrounded by a shell with one complete whorl. It has a rounded body and measures up to 1150μ in length.

Among the most obvious external characteristics are the velar lobes, the foot which is extended over the whorl of the shell, the operculum, and the larval heart. The velar lobes measure up to 800μ from lobe to lobe and are bordered by cilia 47μ in length. These are the main locomotory organs and can be folded, twisted, and contracted by the larva. The foot is completely ciliated and has several tactile bristles 3μ in length on the tip. The operculum now present is thin, clear, fragile and does not extend beyond the foot. At full expansion, the larval heart occupies most of the mantle cavity and extends into the right pleural region. The beat is irregular. The velum, foot, and heart extend out from the shell (Figure 8).

The ventral mouth lies between the velar lobes, is completely ciliated and leads to a ciliated esophagus. The esophagus enters the gastric stomach on the ventral side. There is an oral ciliary band ventral to the mouth, extending between the larval kidneys.

The adult kidney in the pleural groove is yellow and ovoid in shape. The larval kidneys are still present behind the velum.

Both statocysts are completely developed and are dorsolateral to the mouth.

The columella muscle is well defined and has 2 shell attachments. Additional musculature is obscured by yolk.

Advanced veligers usually lie on their side, either right or left, so that one velar lobe is positioned down and the other up. Occasionally they are found lying on their dorsal side so that the velar lobes are widespread and the mouth can be seen. This positioning has to do with the bulkiness of the shell. Movement is clumsy and mostly rotational.

DISCUSSION

Identification of veliger characteristics in this paper is based on the work of D'Asaro (1966) on *Thais haemastoma floridana* which has a planktotrophic veliger stage. Early larval development of *T. emarginata* is similar to that of *T. haemastoma*. The most evident variation is in the development of the protoconch and operculum. Both of these structures appear earlier in *T. haemastoma* development.

Because of the large yolk reserve, the egg diameter and advanced veliger stage of *Thais emarginata* are larger than the egg and corresponding veliger after the first planktotrophic stage of *T. haemastoma*. The amount of yolk reserve in *T. emarginata* is surprising and makes organogenic work difficult without resorting to histological techniques.

According to Ricketts & Calvin (1968) there is not enough yolk to maintain the embryos through hatching time. "Consequently they eat each other until only one – and that one presumably cock of the walk – is left to emerge from the capsule into a world where its chances of survival are still poor" (Ricketts & Calvin, 1968: 212). While this may be true in some cases, it was observed in the present study that as many as 16 larvae develop to the crawling stage and hatch from the egg capsule. Embryos do ingest all of the available nurse eggs, but further growth seems to be at the expense of their own yolk reserve. Only twice was cannibalism observed, and this occurred with embryos removed from the egg capsule.

A peculiar feature in the growth pattern of *Thais emarginata* was observed in 21 of 85 (25%) capsules. Veligers contained within a single capsule tended to vary in size or stage of development or both. The greatest developmental range was found in a capsule containing 10 veligers. Six of these were advanced, 2 were third stage, and 2 were second stage. Whether the dissimilarities were due to differences in feeding rates, fertilization times, or simply to individual developmental rates was not determined.

ACKNOWLEDGMENTS

It is with pleasure that I acknowledge the help of Dr. James Blake and Mr. David Montgomery who gave invaluable advice on observation procedures and critized this manuscript. My thanks also go to the National Science Foundation for financial support derived from N. S. F. Grant GB-19344.

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